Darwin's Theory of Sexual Selection is Not Wrong, Just Far from the Full Story

By Sarah B. Hrdy 1, 844 words

Comments on "Causes, Contexts and Consequences of Human Sexual Dimorphism", an Invited Poster Symposium organized by Holly Dunsworth and Cara Wall-Sheffler at annual meeting of American Association of Physical Anthropology, April 11-14, 2018 in Austin, Texas

Half century ago when mine became the first class of Radcliffe women awarded Harvard degrees, Harvard College did not then have a single tenured woman professor since the only one, Cora Dubois, had retired the year before. Besides taking over University Hall to protest the Viet Nam war the other distinguishing feature about the class of '68 was that we were the first women allowed access to Lamont undergraduate library, formerly reserved for men only. In 1970 when I returned for a PhD, I became my advisor Irven DeVore's first woman grad student. Look around you – a lot has changed since then.

But its not only the genderscape of Evolutionary Anthropology that has changed. As demonstrated by the posters today, there has been a dramatic expansion in Darwinian fields of vision, especially when it comes to theorizing about sex differences. My job today is to put this transformation in historical perspective. It was during the 1970s that Darwin's long overlooked ideas about male-male competition and female choice laid out in *Descent of Man and Selection in Relation to Sex* in 1871, began to resurface and thanks to Robert Trivers become linked to another forgotten paper, a 1948 report on drosophila genetics by Angus John Bateman where he argued that since male gametes (sperm) were by definition, always smaller and more abundant than larger, scarcer female gametes (ova), there would result "a combination of an undiscriminating eagerness in the males and a discriminating passivity in the females," Extrapolating to humans, Bateman added that "Even in derived monogamous species (e.g. man) this sex difference might be expected to persist as a relic…"

For years afterwards even the best available textbooks in the field like Martin Daly and Margo Wilson's *Sex, Evolution and Behavior* took for granted that "most adult females… are likely to be breeding at or close to the theoretical limit" while "among males by contrast there is the probability of doing better…" (Daly and Wilson 1978:59). Meanwhile Don Symons's 1979 *Evolution of Human Sexuality,* developed these views into the founding document for the emerging field of Evolutionary Psychology.

Fast forward four decades. By now it is abundantly clear that females are far from passive, and their strategizing often results in considerable variance in female

reproductive success. Indeed, under some social or ecological conditions, variance in female reproductive success may exceed that in males, as it often does in cooperatively breeding meerkats or marmosets or in those cercopithecine monkeys where female social positions are both heritable and correlated with age of menarche and offspring survival. Over sequential generations active female agents may be playing for more enduring stakes than males are. Today's top textbooks like Tim Clutton-Brock's *Mammal Societies* or Carel van Schaik's *The Primate Origins of Human Nature*m, both published in 2016, reflect this expanded, more integrative perspective. Carel still concedes that in general, female mammals are likely to invest more in offspring and when they do may sometimes be choosier than males about mating. Carel even gives a deferential nod to Trivers (1972) by reminding us that *in most mammals "*males compete for matings, females compete for whatever it is that limits the production of surviving offspring (usually resources such as access to food and shelter*)". But* he also stresses, this is *not* a universally applicable principle -- especially in the case of primates where females can often benefit from mating with multiple males, including when not actually fertile (2016:145). As with Erin Vogel, Jason Kamilar and Jessica Rothman's poster today, Carel devotes much attention to male and female feeding ecology and energetics. Energetics loom larger still in Tim Clutton-Brock's textbook. I counted 13 separate entries to it. Tim specifically reminds us that in addition to Operational Sex Ratios and Bateman gradients, we need to take into account "social and ecological factors affecting the costs and benefits of investment in breeding opportunities" (Clutton-Brock 2016:14)

This broader perspective is evidenced in every presentation today. There is increased recognition of how multi-faceted, typically dynamic, not to mention dialectical underlying processes and feedback loops shaping sex differences can be. Darwinian Natural Selection and Sexual Selection and also we now increasingly realize, *other processes as well*, such as social selection favoring competitive females or gender-differentiated parental investment as Katie Hinde outlined. Such processes play out against varying backgrounds with different resource availability or demographic histories and involving variable metabolic loads. In the human case, local economics with both divisions of labor and increasingly influential social norms synergistically interact with biology as Ashley Davoe, Mary McAlpine and Molly Zuckerman illustrated using analyses of skeletal assemblages from different human populations.

Today's explanations for sexual dimorphism range far beyond a single-minded focus on male-male competition and female choice for the genetically "best male" to mate with. That said, I would be the last person to suggest that we set aside Darwin's highly original ideas pertaining to sexual selection. Unquestionably, nature offers many circumstances where reproductive competition between

between males for access to females, but now clearly occurring in either sex, results in some individuals being big winners, other breeding less, or not at all. Among primates, male-male competition can plays out in drastic ways, as in the case of over 50 species of primates where males who succeed in usurping control of a breeding group eliminating the progeny of the last male a mother mated with, distorting her reproductive options going forward.

Darwin's theory of sexual selection continues to provide a powerful framework for understanding phenomena such as infanticidal tendencies or increased muscle mass or bigger canine teeth in males compared to females. If broader samples of *Australopithecus afarensis* continue to suggest more monomorphic male and female body sizes than in modern gorillas, Philip Reno's hypothesis that these australopiths were characterized by more moderate competition between males for mates remains reasonable, although it might be a good idea to keep in mind other possibilities, such as (taking chimpanzees as an example) a female who stops growing so soon that she is outsized by competing females eat her baby, might find herself disadvantaged. Similarly, David Puts can feel relatively confident arguing that intra-male competition helps account for deep baritone voices and bushy facial hair in their human male descendants even though as Hodges and company (with Richardson, Weinberg, Gurven, and Gaulin) point out, *female choice* need not be involved. Nor is it wrong to continue to point out that across mammals greater female investment in offspring is likely – *albeit far from guaranteed* – to produce situations where fertile females are a key limiting resource. The point so nicely made by the posters today however is that sexual selection is *far from the whole story*.

Darwinian sexual selection theory is definitely *not* wrong, as Joan Roughgarden and others like to argue. It is simply woefully incomplete to explain the full range of sexually dimorphic traits. As Holly Dunsworth and Cara Wall Sheffler urge, we need to keep in mind additional factors – activity budgets, growth trajectories, metabolic costs, especially maternal outlays during gestation and lactation, as well as myriad other situation-dependent factors and conditions. Daunting as such factors may be to measure, considering them generates new questions, often requiring new tools and avenues of research such as those being pursued by Holly Dunsworth, Helen Kurki, Cara wall-Sheffler, Erin Vogel, Jessica Rothman, Rachel Voyt, Rebecca Lewis.

Where sexual selection theory really falls short is in trying to account for sexual dimorphisms in humans. Divisions of labor, culturally sanctioned gender roles, ideals and stereotypes can all constrain female autonomy and exercise profound effects on phenotypic development through different diets, exposure to morbidity and mortality. Cultural prescriptions constrain free movement and

foraging patterns, dictate residence patterns and undermine economic prospects especially for women. What Liz Ortiz, Adam Zimmer, Pamela Stone and Ryan Harrod refer to as culturally-specific "proper behavior" prescribed for each sex can drastically distort mate choice and reproductive autonomy, particularly for women. As Liz and company point out, these "sex and gender identities are socioculturally constructed and historically contingent". Going forward, I think its possible that taking into account differently timed Somatic Reproductive Effort and Behavioral Reproductive Effort as proposed by Ellison and Richard Bribiescas propose, may help us in idenfitying and assessing these effects. I agree with them that SRE and BRE are complementary processes, but its also worth noting when these processes diverge, as for example in the case of "hard-workng" post-menopausal women.

No doubt, expanding theory to better encompass the full range of pressures on both sexes took longer than ideally it should have. But after a century and a half we are emerging with a much more multi-dimensional and integrated understanding of sex differences. And yes, there can be little doubt that enhanced diversity in the community of researchers played a role. However I resist the temptation to view this as a victory for feminism or any other –*ism*. The fact is whenever longstanding biases are identified and corrected, its science that come out ahead.

This leads me to my final point. Neither my generation, nor yours today, was the first to recognize and point out how androcentric and in need of expansion Darwinian theories were. No sooner was the *Origin of Species* published than a handful of distaff Darwinians stepped forward to identify androcentric biases. Years after I had published *The Woman that Never Evolved*, it was really humbling to discover that a century earlier, Darwin's French translator Clemence Royer who I had never even heard of before, had made many of the same points I had, arguing that "Up until now science, like law, has been exclusively made by men and has considered women too often an absolutely passive being, without instincts or passions, or her own interests." (1874).

The point is, even same biases get identified and even corrected, curiously androcentric viewpoints have this insidious way of creeping back in. Witness a 2015 cover story for *Time Magazine* written by the evolutionary psychologist David Barash where he reminds readers that "for men, the underlying evolutionary calculus of polygamy is clear: the possibility for a larger number of offspring and thus enhanced evolutionary fitness. For women, the reason is more nuanced: The possibility of better genes for their children, improved access to material resources and social advancement. *It can be argued that a woman would be better off as the 20th wife of a very wealthy man than as the only wife of a pauper…"*[1] No mention is made of constraints on female autonomy or earning power that might constrain mothers to depend on resources

provided by a man. Such recidivism is why its worth keeping in mind how readily thresholds for accepting certain assumptions, perhaps especially assumptions about sex difference, can be colored by cultural stereotypes, lived personal experience not to mention personal convenience and, let's face it, some individual's professional self-interest. Conflicts of interest between the sexes along with primate tendencies to perceive males and females differently long pre-date the emergence of the genus *Homo*. We would do well to keep this history in mind, cautioning us about the sorts of biases we should be alert to.
